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Climate-driven synchrony in growth-increment chronologies of fish from the world's largest high-elevation river

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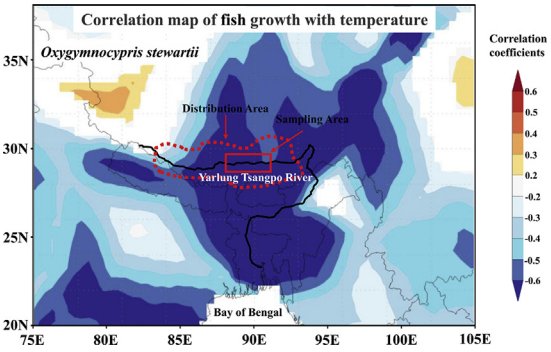
HIGHLIGHTS

- Fish growth-environment relations were established in a river fed by glacial water.
- Growth chronologies of fish were established using dendrochronological methods.
- Fish chronologies were negatively correlated with air temperature.
- Higher trophic level (TP) fish were more sensitive to climate than lower TP fish.

GRAPHICAL ABSTRACT



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ABSTRACT

Understanding how sensitive aquatic ecosystems respond to climate change is essential for effective biodiversity conservation and management. The Tibetan Plateau (TP) is one of the most globally sensitive areas to climate change with potentially serious implications for resident fish populations and aquatic food webs. However, how the growth of TP fish responds to climate change, and how this response varies with the trophic level of different species remain unknown. We established growth-increment chronologies of two important Schizothoracinae fishes that are endemic to the TP (e.g., the omnivorous *Schizopygopsis younghusbandi* and the carnivorous *Oxygymnocypris stewartii*) from the Yarlung Tsangpo River, using otolith increment width measurements and dendrochronological methods. These growth chronologies were correlated with key indicators of environmental variation (temperature, precipitation, and river discharge) to examine the potential effects of climate change. The two chronologies displayed synchronous responses to recent climate change. In this glacial-fed river, the growth of both fish species was significantly and negatively correlated with the mean annual air temperature, while it was positively but not significantly correlated with precipitation and discharge. The higher trophic level species *O. stewartii* was more sensitive to climate than was the lower trophic level species *S. younghusbandi*, with temperature variables explaining a higher proportion of growth variability in *O. stewartii* (64.6%) than in *S. younghusbandi* (46.4%). The results collectively indicate that both species are highly sensitive to climate change, which may affect fish growth by altering water environment, fish physiological fitness and food availability. This study provides further empirical evidence of the utility of growth-increment

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chronologies for investigating the effects of climate change on aquatic ecosystems across different basins and water body types of the TP. These findings can inform conservation and management actions related to addressing climate change on the TP and other high-elevation temperate systems found worldwide.
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1. Introduction

Climate change and its environmental consequences have been widely observed and acknowledged (Walther et al., 2002; Parmesan, 2006; IPCC, 2014). Understanding how sensitive ecosystems respond to climate change is essential for effective conservation and management, and can provide sentinels for changes in other ecosystems (Adrian et al., 2009). The Tibetan Plateau (TP), which is commonly known as the third pole because of its massive size and high altitude (total area 2,500,000 km^2, average elevation >4000 m a.s.l.), is one of the most sensitive areas in the world to climate change (Kang et al., 2010; Tao et al., 2015; Tao et al., 2018). The warming rate of this region was twice that of the global average during the period of 1960–2012 (IPCC, 2014; Tibet Regional Innovation Team, 2015). The TP stores and cycles vast amounts of water resources in various forms, such as rivers, lakes, glaciers, snow cover and permafrost (Ma et al., 2011; Yao et al., 2012; Cuo et al., 2014). Climate warming has intensified the global water cycle (Huntington, 2006), thereby resulting in substantial environmental changes in the extent and characteristics of aquatic ecosystems (i.e., lakes and rivers) in this area. For example, >80% of lakes increased in area between the 1970s and 2010 (Zhang et al., 2014a). The flow regimes (i.e. magnitude, timing, frequency, and duration of flow events) of all major rivers have been affected by climate change to varying degrees (Cuo et al., 2014).

Such environmental changes not only threaten the water supply for 1.4 billion people on and around the TP (Immerzeel et al., 2010) but also alter aquatic ecosystems at all levels of organisms, and across the entire food web. More specifically, warming can stimulate increases in primary production (including the growth of benthic algae and phytoplankton) in lakes and rivers (Allan and Castillo, 2007; Adrian et al., 2009). Lake area expansion and increasing surface runoff from precipitation or melting water can also increase the input and availability of allochthonous organic matter (e.g., terrestrial plants and arthropods) in lakes and rivers (Vannote et al., 1980; Doi, 2009). These terrestrial carbon sources are an important subsidy to aquatic food webs and may increase due to the warming and wetting of the TP (Xu et al., 2007; Chen et al., 2013). In recent decades, the combination of changes in the temperature and precipitation regimes significantly increased net riparian primary production in the TP region (Fan et al., 2010; Zhang et al., 2014b). Consequently, the increasing of primary production could accelerate the growth of aquatic consumers such as fish. At present, it is largely unknown how climate-induced changes in aquatic primary production and terrestrial carbon subsidies to aquatic food webs will affect fish growth in the TP.

Growth chronologies of fish derived from regular growth increments (i.e. annuli) in carbonate body parts (e.g. scales and otoliths) have increasingly been used to study fish responses to climate change (Black et al., 2005; Morrongiello et al., 2012; Doubleday et al., 2015). Growth chronologies can provide a long-term continuous record of environmental changes which is often lacking from traditional biological monitoring data (Gillanders et al., 2012). Two common dendrochronological techniques, i.e. crossdating and detrending, are critical in building growth chronologies. Crossdating assures that each increment is assigned to the right calendar year and provides a mean to assess the quality of dating (Black et al., 2016). Detrending aims to remove the intrinsic effects (e.g., from age or size) on increment width series from the extrinsic effects (i.e. from the environment) before establishing a growth chronology (Weisberg, 1993; Cyterski and Spangler, 1996; Weisberg et al., 2010). The annual increment width displays an intrinsic decreasing trend with age or size. Only once this intrinsic trend is eliminated (i.e., detrending) can the extrinsic effects on the annual increment width series or master growth chronology be examined. The established master growth chronology can not only be used to investigate the effects of environmental change on fish growth (Black et al., 2008; Rypel, 2009; Tao et al., 2015), but also be used for environmental reconstruction (Black et al., 2009), age validation (Black et al., 2005), detecting changes in reproductive phenology (Tao et al., 2018), and exploring synchronous responses across ecosystems (Black, 2009; Izzo et al., 2016; Ong et al., 2016). Climate change induces alterations in freshwater fish growth, and these can be habitat-specific (e.g., lotic vs lentic) alterations (Richard and Rypel, 2013; Tonkin et al., 2014); changes in fish growth can have distinct impacts based on the trophic level positioning of each species (Voigt et al., 2003; Thackeray et al., 2016). For example, climate change can decrease bottom-up trophic cascade effects along the food chain, and these effects can be delayed in higher predators (Thompson and Ollason, 2001; Frederiksen et al., 2006).

Here, we studied the climate change response of two endemic fish species in the world's highest elevation large river and one of the most climate-change sensitive catchments on the TP (You et al., 2007; Zhang et al., 2014b). Our specific objectives were to establish growth index chronologies of the omnivorous *Schizopygopsis younghusbandi* Regan, 1905 and the carnivorous *Oxygymnocypris stewartii* Lloyd, 1908 from the Yarlung Tsangpo River based on annual increment width measurements of otoliths and to investigate the effects of climate change on the growth of fish at different trophic levels over time. The outcomes of this study provide information on how riverine fish at different trophic levels respond to climate change on the TP and how these responses differ in fish from other water-body types (e.g., lakes) in this area. This study will provide essential insights for future aquatic ecosystem management and conservation to help cope with climate change on the TP and other high-elevation temperate systems around the world.

2. Methods

2.1. Study species

Schizopygopsis younghusbandi is one of the most important local commercial fishes and is only distributed in the middle reaches of the Yarlung Tsangpo River (Duan et al., 2014). During a fish survey conducted from 2004 to 2006, *S. younghusbandi* contributed to 30% of the total captures (Chen and Chen, 2010). This species is omnivorous and mainly feeds on periphyton algae and macrophytes, as well as on some invertebrates and their eggs (Ji, 2008). It can live up to 20 years (Chen et al., 2009; Duan et al., 2014), and males and females sexually mature at four and seven years of age, respectively (Duan, 2015).

Oxygymnocypris stewartii is the top predator fish in the Yarlung Tsangpo River. Due to rapid population degradation, this species was listed as an endangered species (Yue and Chen, 1998). During the survey (Chen and Chen, 2010), *O. stewartii* accounted for 8% of the total captures (Jia and Chen, 2011). The main food sources of *O. stewartii* are invertebrates as well as larvae and juveniles of other endemic or alien fish species, including *S. younghusbandi* and *Carassius auratus* (Ji, 2008). The longevity of *O. stewartii* is approximately 20 years, and males and females reach sexual maturity at five and seven years of age, respectively (Huo, 2014).

2.2. Field sampling and otolith section preparation

Specimens of *S. younghusbandi* and *O. stewartii* were collected in July 2015 and from March to April 2016. A total of 313 *S. younghusbandi* and 57 *O. stewartii* were collected using a triple-layer gillnet and electrofishing gear along the main stream of the Yarlung Tsangpo River (Table 1). Otoliths were removed from the utricle, cleaned and dried, and then stored in labelled polyethylene tubes. Otoliths were individually embedded in resin and cured in an oven (50 °C) for 2 h (Tonkin et al., 2014). Then transverse otolith sections were cut using a modified high-speed gem-cutting saw with a 250-μm thick diamond-impregnated blade. Thin sections (250–300 μm) were cut along a line from the primordium through the most uniform posterior-dorsal axis. The sections (typically, three sections close to the primordium were taken from each otolith) were then mounted on a microscope slide under a glass cover slip.

2.3. Increment width measurement, crossdating, and establishment of master growth chronology

The best section of each otolith was photographed using a charge coupled device (CCD) digital camera mounted onto a dissecting microscope (Leica MZ80) with transmitted light and different magnifications (×25 to ×50) based on the section size. The annuli on otoliths of both *S. younghusbandi* and *O. stewartii* were validated using marginal increment ratio analysis (Jia and Chen, 2009; Duan et al., 2014). Unclear sections and those with blurry annulus boundaries were discarded for subsequent age determination and measurement. Each section with clear annuli was aged twice with at least a one-week interval between estimations; moreover, both estimations were conducted by the same viewer. A third read was conducted with re-examination if the previous two reads were different. If no further agreement was reached, the section was eliminated. Combined with information on sampling dates, the annuli of aged sections were visually assigned to their respective calendar years using the 'list year' technique (Yamaguchi, 1991). The 'list year' aligns each annual increment into the appropriate calendar year of the formation by subtracting the age from the collection year. Next, the annual increments were measured, in most cases, along a straight line from the primordium to the dorsal margin. Increment width series were measured using Image J software (Schneider et al., 2012) and the 'IncMeas' plugin (Rountrey, 2009). After measurement, all visually cross-dated increment width series for each species were statistically checked using COFECHA (a program developed by Richard L. Holmes and obtained from http://web.utk.edu/~grissino/software). The first increments (birth year) were discarded because the width largely depended on the birth date but not on the corresponding annual environmental variables. Only the width series with at least six increments were kept for the statistical crossdating to ensure that each series was long enough for detrending. In COFECHA, each series was detrended using a cubic spline. Each series was standardized and then correlated with the average of all other standardized series. All correlation values were averaged to obtain the value of interseries correlation. The final 50% frequency cut-off of the cubic spline was set at 22 years for *S. younghusbandi* and 20 years for *O. stewartii*, according to the mean series length and the value of interseries correlation (Black et al., 2005; Tao et al., 2015). Any potential cross-dating error identified in COFECHA was checked and confirmed or corrected by re-examining the otolith sections. Samples with negative or low correlations (Pearson's correlation coefficients < 0.1) with all the other standardized series were excluded from further analyses because these individuals would generate noise and obscure the response pattern of the entire population (Tao et al., 2015). The 'list year' method provided a first-level ageing control for the dataset, while COFECHA was mainly used to identify any potential cross-dating errors and negatively or poorly correlated series in short-lived species (Matta et al., 2010; Tao et al., 2015). Detrending was conducted to remove the intrinsic decreasing trend in the annual increment width with age or size and the development of the master growth index chronology using ARSTAN (a program developed by Edward D. Cook and Paul Krusic and obtained from http://web.utk.edu/~grissino/software). First, each increment width series was detrended with a negative exponential function. We chose a negative exponential function for detrending and not a cubic spline (as during crossdating) because a negative exponential function has been shown to better capture environmentally induced variability in fish growth (Matta et al., 2010). Second, all detrended increment width series were averaged using the biweight robust mean, which can weaken the effects of outliers (Cook, 1985), to form the master growth chronology.

Table 1
Length and weight details of *Schizopygopsis younghusbandi* and *Oxygymnocypris stewartii* samples collected from the Yarlung Tsangpo River in 2015 and 2016.

Fish name	Sampling date	Sample size	Total length range (mm)	Total weight range (g)
Schizopygopsis younghusbandi	July 2015	88	157–428	33–673
	March–April 2016	225	115–453	13–683
Oxygymnocypris stewartii	July 2015	14	269–470	155–833
	March–April 2016	43	233–512	83–1395

2.4. Environmental data and relationships with master growth chronologies

Total annual discharge data at the Yangcun hydrologic station (which is the closest station to our sampling sites) were obtained from publications (Luozhu et al., 2011; Wang et al., 2016). Water temperature data were not available; thus, air temperature data were used as a substitute. Air temperature and precipitation data at the nearby Xigaze meteorological station were obtained from the China Meteorological Data Service Centre (http://data.cma.cn/). The growing season was defined as the period from April to October (Tao et al., 2015).

Synchrony between the master growth index chronology of each species was evaluated using Pearson's correlation. Correlations between the master growth index chronologies and the local environmental variables (annual, growing season and monthly scale) were also conducted. These variables included the mean minimum air temperature, mean air temperature, mean maximum air temperature and total precipitation. One-year lag effects of environmental variables on chronologies were also evaluated by correlation analysis. Spatial relationships between chronologies and key environmental variables were mapped using KNMI Climate Explorer (Trouet and Van Oldenborgh, 2013). Principal component regression (PCR) was used to avoid collinearity problems among environmental variables and to gain a better understanding of their effects on the chronologies (Jolliffe, 1982). In the PCR analysis, all local environmental variables (annual or for the growing season) were entered to generate principal components with an eigenvalue >1. To minimize the effects of occasional outliers, only the chronology parts with a sample depth (number of individuals used for calculation of the growth index for each year) ≥ 10 were used in correlation and regression analyses (Tao et al., 2015).

3. Results

3.1. Master growth chronologies of the two fishes

In total, 55 and 41 otolith samples were successfully used to establish the master growth chronologies of *S. younghusbandi* and *O. stewartii*, respectively (Table 2). Most *S. younghusbandi* samples ($N = 258$) were excluded, mainly because of the low annulus clarity ($N = 140$), followed by a short increment width series or small age ($N = 111$), and low correlation ($N = 7$). For *O. stewartii*, ten samples were excluded because of a short increment width series or small age, four samples were excluded because of low clarity, and two samples were excluded due to low

Table 2
Properties of master growth chronologies for *Schizopygopsis younghusbandi* and *Oxygymnocypris stewartii* from the Yarlung Tsangpo River.

Species name	Sample size	Mean sensitivity	Interseries correlation	Mean series length (yr.)	Autocorrelation
Schizopygopsis younghusbandi	55	0.215	0.563	8.1	−0.014
Oxygymnocypris stewartii	41	0.214	0.415	9.7	−0.056

Sample Size: the number of increment width series used in the chronology development. Mean sensitivity: an index of high-frequency variability. Interseries correlation: an index of the synchrony of the time series used in the chronology development, which is calculated by averaging the correlation between each detrended time series and the average of all other detrended time series. Mean series length: average length of time series used in the chronology development. Autocorrelation: an index of the previous year's effects on growth in the current year.

correlation. The increment width of the two species had comparable sensitivity to inter-annual environmental variations, which were revealed by the mean sensitivity of the master growth chronologies (Table 2). The interseries correlation of both species showed obvious synchrony, although *S. younghusbandi* was higher (interseries correlation = 0.563) than that of *O. stewartii* (0.415). The mean series length of all *O. stewartii* series (9.7 years) was slightly longer than that of *S. younghusbandi* (8.1 years). Moreover, the one-year lag autocorrelations of the master growth chronology were small for both species (Table 2).

The master growth chronology of *S. younghusbandi* spanned from 1996 to 2012, with the period of 2003–2012 having a sample depth of at least 10, while the master growth chronology of *O. stewartii* spanned from 1999 to 2012, with the same period having a sample depth of at least 10 as *S. younghusbandi* (Fig. 1). The confidence interval width of the master growth chronologies decreased as the sample depth increased over time for both species (Fig. 1). The master growth chronologies of the two species showed a high degree of synchrony (Figs. 1, 2003–2012, $N = 10$, $r = 0.603$), although the relationship was not statistically significant ($p = 0.065$).

3.2. Relationships between fish master growth chronologies and environmental variables

The master growth chronologies of both species were negatively and significantly correlated with only the annual mean air temperature, while the effects of annual discharge and precipitation were slightly positive but not statistically significant ($p > 0.05$, Table 3). The r value for the annual mean air temperature and master growth chronology of *S. younghusbandi* was −0.681 (N = 10, $p = 0.030$) and − 0.779 (N = 10, $p = 0.008$) for *O. stewartii*. No lag effect was found between the growth chronologies and the annual or growing season scale environmental variables except the annual mean minimum air temperature with the chronology of *S. younghusbandi* (Table 3).

Significant and negative correlations between the growth chronologies and temperature were identified in the correlation maps (Fig. 2a, b), while correlations between chronologies and precipitation were positive but not significant (Fig. 2c, d). The correlation maps also revealed that these relationships were relatively stable in both fishes' distribution ranges. These correlation maps were highly consistent with the correlation results shown in Table 3.

Significant correlations ($p < 0.05$) between the chronologies and monthly resolved environmental variables were found only during the growing season (i.e., April–October) (Fig. 3a, b). Most of the monthly temperature variables were negatively correlated with both chronologies (Fig. 3a), while most of the precipitation in the growing season months was positively correlated with the two chronologies (Fig. 3b).

In PCR analysis, two principal components were extracted. The first component (PC1) captured 63.6% of the variation (eigenvalue = 5.7) and was associated with most temperature variables. The second component (PC2) captured 27.2% of the variation (eigenvalue = 2.4) and was more related to discharge and precipitation (Table 3). Neither of the principal components were successfully entered into the linear regression with the chronology of *S. younghusbandi* ($p = 0.16$). Rather, only the annual mean air temperature, which had the highest explanation, was used to explain the variability of the *S. younghusbandi* chronology (Table 3, $R^2 = 46.4\%$, $p = 0.030$). In contrast, the 64.6% variability of the *O. stewartii* chronology can be explained by PC1 in the linear regression model (Table 3, $p = 0.005$).

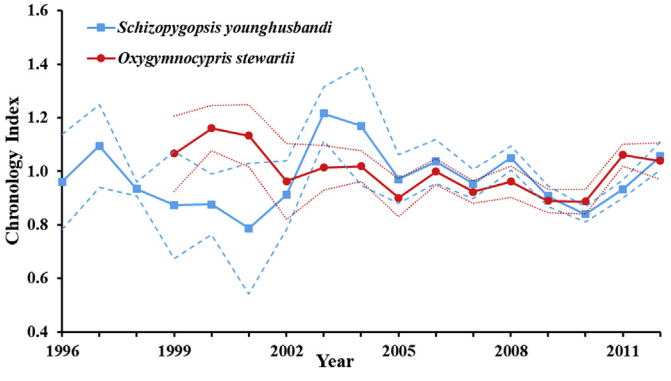

Fig. 1. The master growth chronologies of *Schizopygopsis younghusbandi* and *Oxygymnocypris stewartii* from the Yarlung Tsangpo River. Dashed lines above and below each chronology show corresponding 95% confidence intervals.

4. Discussion

4.1. Fish growth sensitivity and response patterns to climate

This study revealed that the growth of two riverine fishes occupying different trophic levels from the Yarlung Tsangpo River was sensitive to climate and displayed high synchrony with each other (2003−2012). This sensitivity to climate is not unexpected. First, both *S. younghusbandi* and *O. stewartii* are endemic to the TP, and their limited distribution ranges (i.e., occurring only in the middle reaches of the Yarlung Tsangpo

Table 3
Correlations between fish master growth chronology (sample depth ≥ 10) and local environmental variables, and first two principal components (PC1 and PC2) from the Yarlung Tsangpo River. Also shown are environmental variable loadings of the first two principal components used in the regression analysis. SY, *Schizopygopsis younghusbandi*; OS, *Oxygymnocypris stewartii*; SYLag1 and OSLag1 chronologies were used to detect any one-year lag effects of these environmental variables. Anu, annual; GS, growing season (April–October); Dis, discharge; MinT, mean minimum air temperature; MeaT, mean air temperature; MaxT, mean maximum air temperature; Pre, precipitation.

Variable	Variable loading		SY	OS	SYLag1	OSLag1
	PC1	PC2	*r*	*r*	*r*	*r*
Anu Dis	−0.686	0.657	0.521	0.264	0.053	−0.123
Anu MinT	0.668	0.637	−0.389	−0.791**	−0.724*	−0.370
Anu MeaT	0.969	0.174	−0.681*	−0.779**	−0.626	−0.184
Anu MaxT	0.936	0.088	−0.607	−0.598	−0.526	−0.180
GS MinT	0.597	0.717	−0.369	−0.685*	−0.378	0.116
GS MeaT	0.920	0.243	−0.633*	−0.773**	−0.462	0.039
GS MaxT	0.962	0.050	−0.552	−0.646*	−0.366	−0.059
Anu Pre	−0.655	0.706	0.366	0.234	0.200	−0.031
GS Pre	−0.660	0.702	0.367	0.238	0.199	−0.027
PC1			−0.523	−0.804**	−0.576	−0.134
PC2			0.394	0.160	0.069	−0.058

Significant correlations ($p < 0.05$) are indicated.
* $p < 0.05$.
** $p < 0.01$.

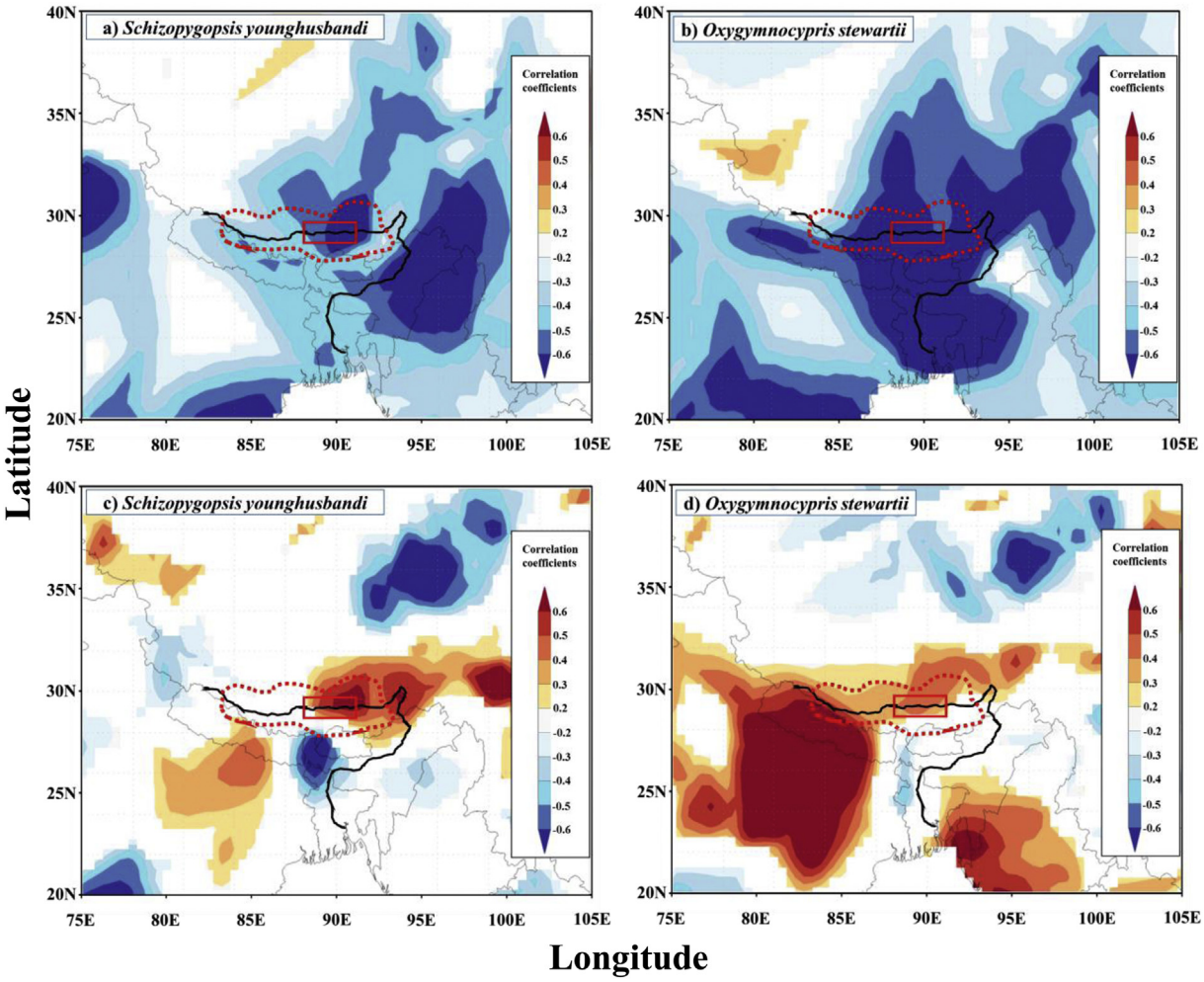

Fig. 2. Correlation maps of fish chronologies with annual mean air temperature (a, b) and annual total precipitation (c, d) for *Schizopygopsis younghusbandi* (left panels) and *Oxygymnocypris stewartii* (right panels). Correlation analysis was based on data from 2003 to 2012. Bold black lines show the Yarlung Tsangpo River, red dashed lines show the distribution of two fish, and red squares show the sampling area. Warmer colors indicate positive correlations, and cooler colors indicate negative correlations. Maps were generated from KNMI Climate Explorer.

River) indicate a relatively small tolerance to environmental conditions (Chen et al., 2009; Jia and Chen, 2009). Second, the harsh living environment and the strong seasonality of the thermal and hydrologic regimes could rapidly influence primary production, and thus, fish growth. For example, the mean annual water temperature of the Yarlung Tsangpo River was between 6 and 10 °C, and the water temperature dropped close to 0 °C in winter and did not exceed 18 °C in summer (Wei et al., 2015). The contents of total dissolved nutrients were very low in this river. For instance, the concentration of nitrate was between 1.3 and 4.3 mg L^{-1} (Huang et al., 2011). The low temperature and nutrient levels may substantially restrict the primary productivity within the river. Consequently, aquatic organisms are facing high environmental stress (e.g., short growing season and low food source availability), and thus, even a subtle environmental change could cause a strong response (You et al., 2007).

The two growth chronologies displayed an evident synchrony (Fig. 2), and both were significantly and negatively affected by the temperature variables (Table 3). The parallel responses of the two fish chronologies at different trophic levels indicate that the local food web is simple or that the climate change affects each species directly rather than through the food web. A more complex food web is likely to buffer or delay the effects of climate change along the food chain, irrespective of whether the effect is in a bottom-up or top-down direction (Steudel et al., 2012). Although no food web study has been conducted for this river, a total of only 13 native fish species indicates that the system is relatively simple (Chen and Chen, 2010). Alternatively, this synchrony can also be expected if climate change directly affects each species rather than affects the species indirectly through the food web (Aebischer et al., 1990).

The higher trophic level *O. stewartii* was more sensitive to climate change than was the lower trophic level *S. younghusbandi*. For example, more environmental variables were significantly correlated with the *O. stewartii* chronology than with the *S. younghusbandi* chronology (Table 3), and the growth variability explained by the environment was higher for *O. stewartii* (64.64%, Table 3) than for *S. younghusbandi* (46.37%, Table 3). The increasing sensitivity to climate change with trophic level has also been reported in other studies (Voigt et al., 2003; Daufresne et al., 2009), and this pattern might be related to the ability of consumers to cope with changes in food resources. More specifically, lower trophic fish often have a wider dietary preference than do higher trophic fish; thus, it is easier for lower trophic fish to adapt to food resource alterations caused by climate change (Rijnsdorp et al., 2009). Consequently, lower trophic fish may spend less energy acquiring food than do higher trophic fish when facing reductions in food resources. Thus, the carnivorous fish *O. stewartii* could be more strongly affected by environmental change than *S. younghusbandi* because *O. stewartii* has a larger forage range and possibly requires a higher forage frequency.

4.2. Possible mechanism of climate effects on fish growth

The growth chronologies of both species were negatively and significantly correlated with air temperature and positively correlated with

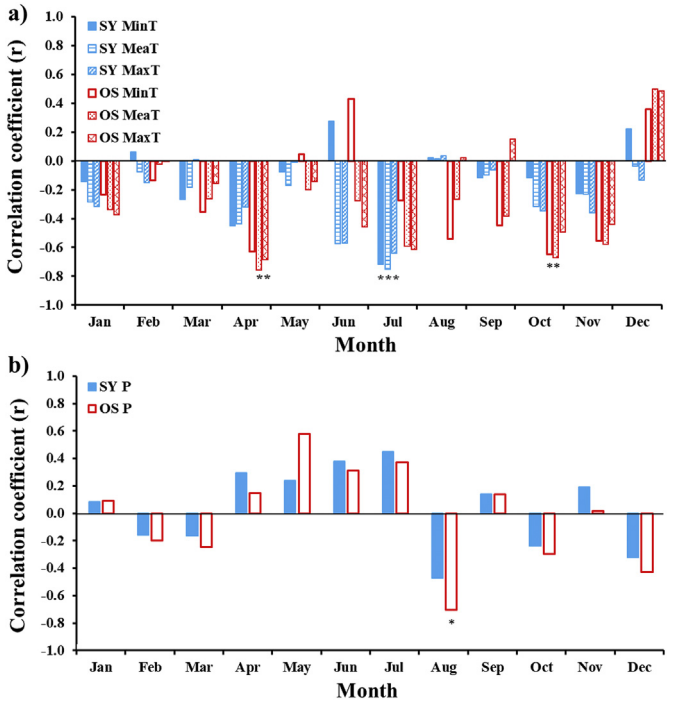

Fig. 3. Monthly variation in correlations between fish growth chronologies and environmental factors for a) monthly mean minimum (MinT), mean (MeaT) and mean maximum (MaxT) air temperature; b) monthly precipitation (P). SY, *Schizopygopsis younghusbandi*; OS, *Oxygymnocypris stewartii*. Correlation analysis was based on data from 2003 to 2012. (*, $p < 0.05$).

discharge and precipitation (Table 3). The significant negative correlations between the fish growth chronologies and air temperature can be explained by the potential water temperature change under climate warming in the Yarlung Tsangpo River. The water supply of the Yarlung Tsangpo River can be significantly affected by snow, glacial melting and permafrost degradation, particularly during the growing season of fish (Cuo et al., 2014). For example, the glacial area in the Yarlung Tsangpo River catchment is 18,161 km^2, accounting for 7.6% of the total catchment area. The mean contribution of melt water to the annual streamflow can reach 32% (Cuo et al., 2014). Therefore, an increase in air temperature can induce water melting from snow, glaciers and permafrost, and consequently, this can cause a decrease in water temperature (Wei et al., 2015). It has been widely documented that water warming can promote fish growth by stimulating the metabolic rate and increasing primary production (Lehtonen, 1996; Neuheimer et al., 2011; Tao et al., 2015). In contrast, a decrease in water temperature can decelerate fish growth by reducing the metabolic rate. Moreover, increased melting water during the spring can also shorten the length of the growing season and, thus, reduce the annual growth of fish.

Alternatively, the negative relationships between fish growth and temperature can also be potentially explained by the decrease in physiological fitness or food limitations when water temperature increases under climate warming. First, fish species in this area are potentially very similar to polar fish species, which have very narrow thermal tolerance windows and are vulnerable to changes in temperature (Reist et al., 2006; Mintenbeck et al., 2012; Comte and Olden, 2017). For example, the upper lethal temperature of some Antarctic fishes is between 4 and 6 °C (Somero and DeVries, 1967). Therefore, coldwater-adapted fish, such as *S. younghusbandi* and *O. stewartii*, could experience a reduction of their physiological fitness under climate warming and, thus, a reduction in their annual growth rate (Neuheimer et al., 2011; Williams et al., 2015). Second, the increased temperature could stimulate fish metabolism, which could only lead to an increase in growth rates with higher food availability. The study river is extremely oligotrophic (Huang et al., 2011); thus, if nutrient availability does not increase with temperature, there can be no increase in primary productivity. Consequently, the increased metabolic rate will reduce the annual growth of fish with limited food availability. However, the relationship between the air temperature and water temperature during the growing season is not clear under current climate change conditions and should be explored through water temperature monitoring in the future. It is also necessary to accumulate more empirical evidence (by observations in nature and by experiments) to examine the relationship between the rise in water temperature and the physiological fitness and behaviour of these two species in the future. For instance, the objectives of these investigations could include understanding the metabolic response patterns of these fishes under warming (Schulte, 2014; Norin et al., 2016), as well as under warming in combination with other environmental stressors (e.g., oxygen depletion; Anttila et al., 2015; Pédron et al., 2017). In addition, investigations on the dynamics of water nutrients and primary productivity under climate warming are highly desired.

The observed correlations between the chronologies and other relevant environmental variables (e.g., river discharge and precipitation) can be explained by variations in food resource availability. River discharge, particularly the surface runoff from precipitation, has a high potential to bring organic matter from adjacent farmland, grassland or other terrestrial inputs; thus, runoff can substantially increase the food source availability for fish (Vannote et al., 1980; Guyette and Rabeni, 1995; Huang et al., 2011). First, these inputs can be direct food for fish, such as terrestrial detritus, leaf litter, and terrestrial insects. Second, the inflow of nutrients or organic matter can promote primary production (e.g., benthic algae) or the growth of aquatic invertebrates, which are autochthonous food sources for fish. Most of the rivers on the TP are dystrophic (Guan et al., 1984), including the Yarlung Tsangpo River (Huang et al., 2011). As a consequence, nutrients are the predominant limitation of primary productivity. Recent anthropogenic activities have significantly changed the land use in this basin, e.g., increased area of construction and forest, but decreased area of grassland and wetland (Maloney and Weller, 2011; Li et al., 2013; Liu et al., 2014). Surface runoff from specific land types and seasons rather than discharge or precipitation could be a better indicator to reflect terrestrial inputs and nutrient inputs (Xia et al., 2016). An accurate estimation of terrestrial inputs could help explain the climate-fish growth relationship in this river. Therefore, we argue that allochthonous and/or autochthonous sources could be a possible cause of the observed variation in the annual growth of *S. younghusbandi*. Although the top predator, *O. stewartii*, does not directly rely on terrestrial detritus or algae, a good year of prey fish (e.g., *S. younghusbandi* and *C. auratus*) may provide more food resources. For instance, abundant food resources are likely to result in enhanced prey fish recruitment success (Burrow et al., 2011), and thus, more prey fish would be available for higher predators. Collectively, changing the availability of food resources could be a possible mechanism responsible for determining how climate change affects the growth of both fish species.

4.3. Different growth patterns in response to climate change for fish from rivers and lakes

This study also indicates that riverine fish and lacustrine fish on the TP potentially display distinct growth patterns in response to climate change. For example, temperature negatively affected fish growth in the Yarlung Tsangpo River but, positively affected fish growth in Selincuo Lake (Tao et al., 2015). In Selincuo Lake, the effects of precipitation on the growth of *Gymnocypris selincuoensis* were negative (Tao et al., 2015), but in the Yarlung Tsangpo River, the impact of precipitation on the growth of *S. younghusbandi* and *O. stewartii* was positive. However, the mechanism underlying the change in fish growth under climate change could be the same in both lakes and rivers. That is, climate change affects fish growth by changing food source availability. In rivers, more food source availability could result from increased

terrestrial inputs with surface runoff (i.e., precipitation). Additionally, an increase in the local air temperature in the Yarlung Tsangpo River catchment could have an inverse effect on primary productivity because increased air temperature could initially reduce river water temperature though increasing ice melting. In lakes where water temperature is positively and significantly correlated with air temperature (Tao et al., 2018), warming can increase the autochthonous productivity within the lake, especially in the lakeshore zone. The difference between the responses of TP riverine fish and lake fish to climate change is another viewpoint to consider when planning conservation and management. More comparable regional and even global studies should be conducted in the future to examine this speculation.

4.4. Limitations

This study has some limitations. The first limitation is the representativeness of the *S. younghusbandi* chronology. The requirement for otolith clarity is much higher in increment width series measurements for chronology development, than for simple annulus counting for age determination. Therefore, we excluded many *S. younghusbandi* otolith sections before chronology construction due to their relatively low annulus clarity, and we assumed that our subset was representative of the broader population. The second limitation is that we did not construct chronologies for different life history stages (Ong et al., 2015). Although no habitat or diet transition between juveniles and adults has been reported for the two species — and no reproduction check was found on the otolith sections of either species — this does not guarantee that juveniles and adults have similar growth responses to climate change (Ong et al., 2015). In this study, it is difficult to build separate chronologies for juveniles and adults because the mean series length was short, and the age at which the fishes reached sexual maturity ranged from four to seven. Third, the relatively short length of the chronologies (i.e., 14–17 years) also hindered the examination of long-term effects of climate change on fish growth. Moreover, a short chronology prevents robust testing of climate-growth relationships because a short-term can only have a relatively narrow range of climatic conditions.

5. Conclusion

Collectively, this study and our previous study (Tao et al., 2015) indicate the feasibility of using dendrochronological methods to explore the influence of climate change on Schizothoracinae fish and aquatic ecosystems across different basins and water-body types on the TP. Understanding how climate change affects fish growth by changing physiological fitness and/or food source availability requires more empirical studies. To further test another hypothesis from this study, whether this high river ecosystem is an autochthonous (i.e., benthic algae) or allochthonous source (i.e., terrestrial organic matter inputs) fuelled river, food web studies using gut content analysis or stable isotope analysis should be conducted in the future. This is the first study to show the effects of climate change on the growth of fishes at different trophic levels in the TP. The results emphasize the high sensitivity of riverine ecosystems of the TP to climate change, and this trend likely applies to other high-elevation temperate freshwater systems around the world. The findings can inform planning local and global conservation and management actions related to addressing climate change. For example, we should give priority to the protection of species occupying higher trophic levels (e.g., *O. stewartii*) because they are more sensitive to climate change.

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